

INHERITANCE OF FEED EFFICIENCY IN LAYING HENS  
MEASURED AS METABOLIZABLE ENERGY INTAKE ADJUSTED  
FOR BODY WEIGHT AND EGG PRODUCTION

By

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Abstract of Dissertation Presented to the Graduate School  
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Three experiments were conducted to study the residual component of metabolizable energy intake, defined as the metabolizable energy intake adjusted for metabolic body weight, body weight change, and egg mass output. Individual records for metabolizable energy intake, body weight, and egg mass were used. Mathematical adjustments of data were achieved by using multiple regression techniques where metabolic body weight, body weight change, and egg mass were the independent variables and metabolizable energy intake was the dependent variable.

In the first experiment, 104 Dekalb hens were used for a 3-week test period. Variation in metabolizable energy intake among individual hens, which could not be explained by the differences in body weights, changes in body weights, and egg mass output was observed.

In the second experiment, 180 hens from six different genetic lines of White Leghorn were used for a 4-week test period. The purpose of this experiment was to examine the differences among the partial

regression coefficients for maintenance and egg mass output, and the overall efficiency among different genetic lines. The pooled data of the six lines showed significant differences in feed utilization. A multiple regression equation was derived for each line. Significant differences among the partial regression coefficients indicated significant differences among the lines in their utilization of metabolizable energy for maintenance.

In the last experiment, 335 pedigreed White Leghorn-type hens were used. The experiment started when the hens were 26 weeks old and lasted for 28 weeks. The purpose was to study the effects of the length of test period, age, and egg mass output on the heritability estimates of the residuals. Heritabilities calculated from sire plus dam components of variance averaged .37, .44, and .57 for the 2-week, 4-week, and 8-week periods, respectively. Heritability estimates were higher for periods when egg mass was at its peak and were lower at older ages, regardless of test period length.

This study shows that the residual has potential as a basis of selection for improving feed efficiency in the laying hen. It will give poultry breeders a specific tool in their selection program for improving feed efficiency.

## CHAPTER 1 INTRODUCTION

Feed efficiency in laying hens is the most important trait for the egg production industry because feed cost is the largest single part of total production cost. Feed cost represents about two-thirds of the cost of egg production.

Until now, the most common source of gain in feed efficiency has been increased production. This is true for most of the feed efficiency gain in animals. Feed consumption in the laying hen is largely accounted for by egg mass output and body weight. Breeders have, therefore, relied upon selection for high egg production to improve feed efficiency as a correlated response to selection (Nordskog et al., 1972; Hagger and Abplanalp, 1978; Bordas and Merat, 1981). Selection for higher egg production has improved feed efficiency of laying birds, mainly because the amount of feed needed for maintenance remained almost constant while egg production increased. In some instances, breeders have attempted to reduce feed required for maintenance as a further means of improving efficiency by selecting for small body size (Nordskog et al., 1972; Hagger and Abplanalp, 1978; Bordas and Merat, 1981).

Feed efficiency is not a directly measurable trait. It is influenced by a large number of physiological and environmental factors which sometimes are confounded with genetic differences (Washburn, 1973). The most common criterion for measuring feed efficiency has been

feed conversion or its reciprocal (Nordskog et al., 1972). Feed conversion is defined as feed input/egg mass output. Feed conversion measurement requires individual feed consumption records which are costly and time consuming. There is an automatic correlation between feed efficiency measured as feed conversion and egg mass (Wilson, 1969). Because of the high cost involved in measuring feed conversion and the high correlation between feed conversion and egg mass, breeders assume that only egg production is worth measuring and selection for high egg production will give a high correlated response in feed conversion (Nordskog et al., 1972).

Improving feed conversion by selection for high egg production and small body size may have limits. Small-bodied birds tend to lay small eggs, which are discounted on most markets of the world. Egg production has become very close to the maximum physiological potential of the bird which is an egg per day and gains in egg production tend to a plateau in the high producing breeds (Bordas and Merat, 1981). Thus, it is of interest to consider that part of the variance in feed intake which is independent of egg production and body size.

The feed consumed by a laying hen is used mainly for the production of egg mass and for body maintenance. Expected feed consumption can be estimated from a multiple regression equation using feed consumption as the dependent variable and body weight and egg mass output as the independent variables (Arboleda et al., 1976; Bordas and Merat, 1981). The residual, which is the difference between feed consumption and the expected feed consumption, is the part of feed consumption independent of body weight and egg mass output. If hens differ genetically in their



ability to digest and metabolize feed, the variation in the residual of feed consumption will have a genetic variance.

Heritability estimates of the residual of feed consumption in the literature are variable; however, generally estimates tend to be moderate to high (Wing and Nordskog, 1982a; Hagger and Marguerat, 1985). Measuring the residual component requires individual feed records as measuring feed conversion does. However, the independence of the residual from body weight and egg mass, as well as the moderately high estimates of heritability of the residual suggests a promising improvement in feed efficiency by using the residual as a measurement of efficiency (Wing and Nordskog, 1982a).

Although there are not many studies available on the residual component of feed consumption as a measurement of efficiency, there are some differences among these studies which might have affected the results obtained. The independent variables ranged between two (Arboleda et al., 1976; Wing and Nordskog, 1982a) and as many as six (Hagger and Marguerat, 1985). The test period ranged between a 4-week period (Bordas and Merat, 1981) to a 50-week period (Bentsen, 1982).

The practical significance of these regression approaches, from a genetic point of view, hinges on the possible use of the regression coefficients as selection criteria. That is, the regression coefficients for maintenance and for egg mass might be used as selection criteria for separately improving maintenance efficiency and production efficiency (Nordskog et al., 1972). A first step would be to obtain evidence that the differences between the regression coefficients have a genetic basis, for example, as measured between lines or other genetic

groups. Bentsen (1982) reported a significant difference between the partial regression coefficient for maintenance of White Leghorn and Rhode Island Red.

In all the available studies on the residual as a measurement of efficiency, feed consumption was the dependent variable. Poultry tend to eat to satisfy their energy requirements if fed ad libitum (NRC, 1984). Dietary energy, protein, density, and volume all have significant effects upon feed consumption (Gleaves et al., 1968). After reviewing the data from 34 published reports, Morris (1968) observed that groups of hens offered diets with different energy levels tend to adjust consumption so as to maintain a similar caloric intake. It is generally recognized among poultry nutritionists that a primary determinant of feed intake is the energy concentration of the diet (Pesti, 1982; Pesti and Fletcher, 1983).

The main goal of this work was to examine the residual technique more thoroughly by using metabolizable energy intake as the dependent variable and metabolic body weight, body weight change, and egg mass output as the independent variables. The objectives were

- 1-To study the relationship between feed conversion, as the most common measurement of efficiency, and the residual component among a group of layers.
- 2-To use the residual to compare the efficiency of metabolizable energy intake among six different genetic lines of layers.
- 3-To compare energy utilization for maintenance and egg production by comparing the partial regression coefficients for maintenance and egg production among six different genetic lines.

- 4-To study the effect of test period length on heritability estimates of the residual component by comparing 2-week, 4-week and 8-week periods.
- 5-To study effects of egg production level and age on the estimates of heritability of the residual.
- 6-To examine the possibility of using partial regression coefficients for improving efficiency for maintenance and egg production separately by estimating heritability of partial regression coefficients of maintenance and egg mass.

## CHAPTER 2 REVIEW OF LITERATURE

Feed represents about two-thirds of the cost of egg production. Breeders have long been interested in increasing egg production efficiency on a genetic level. Yet, quantitative genetic studies focused on individual variation in efficiency have not had enough attention (Nordskog et al., 1972). This is because the measurement and collection of individual feed consumption data is expensive and time consuming (Wilson, 1969).

Feed consumption is largely accounted for by egg mass output and body weight. Breeders have, therefore, relied upon selection for high egg production and low body weight to improve feed efficiency as a correlated response to selection. There is no question that breeders have attained a measure of success by the indirect methods they have used (Nordskog et al., 1972). However, the positive genetic correlation between body weight and egg size as well as the fact that gains in egg production tend to plateau (Bordas and Merat, 1981) emphasize the importance of direct selection for efficiency.

The efficiency of feed utilization is a very involved phenomenon that is influenced by a great number of physiological and environmental, as well as individual differences (Hess and Jull, 1948). Kleiber (1936) discussed some of the problems in breeding for feed utilization efficiency. He suggested that one must study the different factors

which influence feed utilization, and then investigate the genetics of each separate factor. He referred to such factors as appetite, eating capacity, absorption capacity, stimulus for growth, and stimulus of egg production. After reviewing various aspects of feed efficiency Balnave (1974) concluded that variations in basal metabolism, plumage condition or physical activity were likely components of this efficiency.

#### Estimating Feed or Metabolizable Energy Requirement by the Laying Hen

Chickens consume feed primarily to meet their energy requirement (Scott et al., 1976). In laying hens feed consumption is largely accounted for by body maintenance, egg production and body weight gain. Joshi et al. (1949) reported that in New Hampshire hens laying at 72% rate, 71% of the feed consumed was used for body maintenance, 2% for increase in body weight and 27% for the production of eggs.

#### Maintenance Requirement

The metabolizable energy requirements of laying hens may be estimated from regression analysis of laying trial data or by use of avian calorimetry or respiration chambers. These techniques may be used to estimate maintenance requirements (Balnave et al., 1978b). The metabolizable energy requirements for body maintenance can be measured directly only on animals not in production. Calorimetric or respiration chamber estimates of the maintenance requirement of laying hens of a wide range of body weights have been carried out by a number of workers (Mellen, 1963; Balnave et al., 1978b). Both calorimetry and respiration chambers techniques can be used to compare differences among breeds or

lines in their maintenance requirements by using a small number of birds. However, from a practical point of view, neither calorimetric nor respiration chamber techniques can be used to capture differences among a large number of individuals.

Metabolic rate, as measured by oxygen consumption or by calorie production per unit of body weight, decreases as body size increases (Mellen, 1963) and is directly dependent on skin surface area. According to Kleiber (1947), body weight to the power .75 is more directly proportional to basal metabolic rate.

There have been many multiple regression equations developed for laying hens in the literature (McDonald, 1978). These equations were developed by using feed intake or metabolizable energy intake as the dependent variable and body weight, or body weight raised to a power of between .50 to .75, body weight change, and egg mass output in a certain period of time as the independent variables. Change in body weight was not included as an independent variable by some workers (Arboleda et al., 1976; Wing and Nordskog, 1982a). Other workers included temperature (Emmans, 1974) or feather covering condition (Hagger and Abplanalp, 1978).

Using the multiple regression techniques, Byerly (1941) found that body weight raised to the power .653 was the best value representing basal metabolism for the data used. Byerly et al. (1977), after examining a wider range of layers' body weight, concluded that body weight to the power .75 better described metabolic body weight than body weight to the power .653 or 1.

The partial regression coefficients for metabolic weight of Rhode Island Red and White Leghorn hens differed significantly, and testing in respiration chambers indicated different maintenance requirements between the two breeds (Bentsen, 1982). Using respiration chambers to measure energy requirements for maintenance, Farrell (1975) concluded that there were differences between the maintenance energy requirements of hens from Black Australorp, White Leghorn and Australorp x Leghorn.

The differences in maintenance requirements among different breeds or genetic lines could be explained in part as differences in activity, feathering condition (Balnave, 1974), and body temperature (McDonald, 1978). Behavioral differences between efficient and inefficient birds with the same production records were observed by Morrison and Leeson (1978); however, no significant differences were found in body composition.

Estimations of energy loss resulting from activity are difficult to predict. Evidence indicates that the activity heat losses associated with eating and with the mechanical process of egg production in the oviduct are small (Balnave, 1974; van Kampen, 1976). However, other types of activity have a variable effect on heat loss. Differences in temperament, and therefore genotype, plane of nutrition, degree of feathering, and environmental temperature all are important factors in determining activity heat loss (Balnave, 1974).

A considerable amount of the total heat dissipated by the adult bird (15%, according to Sturkie, 1965) arises from the unfeathered head appendages. This is consistent with the reduction (about 2%) of food

intake associated with the pea-comb gene which limits the size of these appendages (Merat and Bordas, 1979).

Any estimate of the maintenance requirement derived using laying hens would include a contribution from ovarian tissue according to Balnave et al. (1978b). This ovarian contribution had been shown to be the result of egg yolk synthesis at maintenance and not to any increase in metabolic rate as a consequence of estrogen secretion by the mature ovary. Balnave et al. (1978a) concluded that birds that had been temporarily out of lay would synthesize egg yolk in ovarian follicles prior to the production of eggs and this would result in an elevated maintenance energy requirement.

#### Egg Production Requirement

Metabolizable energy required for production may be estimated indirectly from the amount of production and the average of feed utilization efficiency of the adult hens. Ovariectomy studies of Balnave et al. (1978b) indicated an efficiency of 75.8%. Metabolizable energy required for egg production also can be estimated from multiple regression equations using as independent variables mean body weight or body weight raised to the power between .5 to 1, body weight change, and egg mass produced during the test period and metabolizable energy intake as the dependent variable (Byerly, 1941).



## Criteria for Measuring Feed Efficiency

### Feed Consumption

According to Nordskog et al. (1972), feed consumption has not been regarded as an effective selection criterion for efficiency of feed utilization in chickens. Both Kondra and Hodgson (1961) and Maijala (1966) reported that feed conversion was not correlated with feed consumption. Wilson (1969) in his study of genetic aspect of feed efficiency in broilers stated that feed consumption, in spite of its part-whole characteristic, was not correlated with feed conversion.

The results reported by Wing and Nordskog (1982b), averaged over two populations, indicated that use of information on individual feed consumption with truncation selection of the top 38% of the population was expected to increase total income over feed costs by 17%. This compared with values of 4 and 9% reported by Hagger and Abplanalp (1978) and Arboleda et al. (1976), respectively.

### Feed Conversion

Efficiency of feed utilization is a major factor of interest to the poultry breeder since it represents about two-thirds of poultry production cost. The most commonly used criterion has been feed conversion or its reciprocal (Nordskog et al., 1972). The cost of individual feed conversion experiments and the high statistical correlation of feed conversion values with production has resulted in a paucity of research data in the area of feed conversion compared to that for production (Nordskog et al., 1972; Washburn, 1973).

Maijala (1966), in a study of performance records, concluded that feed conversion was the best measure of potential genetic efficiency in layers. After two generations of selection for improving feed efficiency in laying hens by using feed conversion as the sole selection criteria, a reduction in body size was observed; however, the incorporation of the egg mass in the feed conversion ratio was effective in preventing a decline in egg number and size (Harris, 1969).

Koch et al. (1963), in a study of feed conversion in beef cattle, pointed out that efficiency is not a directly measurable trait but is solely a function of feed consumption, gain, and time, which produces certain automatic correlation among these variables. These workers proposed, instead of the feed conversion ratio to measure efficiency, the deviation between the individual gain and gain predicted from a regression equation with feed consumed as the independent variable.

Because of the high correlation between feed efficiency, measured as feed conversion and egg production (Nordskog et al., 1972), and because measuring individual feed consumption is costly and time consuming (Wilson, 1969), breeders have relied upon improving feed conversion as a correlated response to selection for high egg production. In some instances, however, breeders have attempted to select for reduction in body size as a further means of improving feed efficiency (Hagger and Abplanalp, 1978).

It has been shown by some studies that selection for production did not result in improving feed conversion as a correlated response. After five generations of selections for high and low body weight at 8 weeks of age in two lines of White Plymouth Rocks, Siegel and Wisman (1966)

found no significant differences between the two lines in feed efficiency (body gain/feed consumption). They concluded that selection for increased body weight when feed was provided ad libitum was largely a selection for appetite. This was in agreement with Lepore (1965) who had reached the same conclusion.

In a study of genetic aspects of feed efficiency in broilers, Wilson (1969) concluded that although the correlation between body weight gain and feed efficiency is part-whole and therefore exhibits a certain automatic property it does not necessarily guarantee a favorable response in feed efficiency as selection changes body weight gain. If the coefficient of variation of feed intake becomes considerably larger than that for body weight gain, one would expect the correlation between gain and efficiency to become unfavorable and selection for body weight gain would increase feed consumption to the extent that the realized body weight gain would not be more profitable.

#### The Residual Component of Feed Consumption

Until now, the most common source of improved feed efficiency has been increased production. This has been true for most of the production traits in domestic animals. But even under standardized environment, differences in production, body weight and weight gain explains only 80-90% of the variation in efficiency between strains of laying hens and 70-90% of the variation between individuals within strains (Bentsen, 1982). Considering the relatively high feed expenses in egg production, it might be of some interest to investigate the

sources of the 10-30% of the variation in efficiency that is left unexplained.

The unexplained variation in efficiency can be thought of as a variation in deviations between observed feed consumption and expected feed consumption when production, body weight, and body weight change are taken into consideration (Arboleda et al., 1976; Hagger and Abplanalp, 1978; Bordas and Merat, 1981). The expected feed consumption can be estimated from a multiple regression equation with feed consumption as the dependent variable and egg mass, body weight or metabolic weight, and body weight change as independent variables. The remaining variability, due to deviations of individual hens from their predicted values, was termed residual food consumption (Arboleda et al., 1976; Hagger and Abplanalp, 1978; Bordas and Merat, 1981) and would require direct measurements of the residual for genetic improvement.

Bordas and Merat (1981) studied the significance of the residual feed component in two brown-egg strains. Expected feed consumption was estimated from a multiple regression equation using as independent variables metabolic body weight (body weight to the power .50), body weight change, and egg mass produced during the test period. The residual was then calculated as observed feed consumption minus expected feed consumption. They reported highly significant differences between sire families for the residual in both strains for females. They stated that little information was available concerning the correlations between residual food consumption and production traits as well as physiological or morphological traits.

The variation in the residual feed consumption might be due to variations in physiological factors such as basal metabolic rate and regulation of appetite (Bordas and Merat, 1981). Genetic variation in residual feed consumption suggested that differences in other related traits, such as feather covering, behavioral traits, energy metabolism, and body composition should be investigated (Hagger and Marguerat, 1985).

Residual feed consumption defined as the observed feed consumption minus the expected feed consumption, where the expectation is from a multiple regression equation containing body weight, or body weight raised to a power of between .50 to .75, body weight change, and egg mass in a certain period of time, also will contain feed wastage. However, the amount of feed lost at the hopper by spillage might have a genetic basis (Nordskog et al., 1972).

Arboleda et al. (1976) found that between 39 and 47% of the total variance of feed consumption could be accounted for by body weight and egg mass. Hagger and Abplanalp (1978) using body weight, body weight change, egg mass, and age at first egg as independent variables reported coefficients of determination between 52 and 72% with a tendency to lower values from older birds. Hagger and Marguerat (1985) added to the independent variables age at first egg and egg composition characteristics as well as body weight, body weight change, and egg mass. They concluded that the inclusion of egg composition characteristics did not increase the accuracy of the predicted feed consumption. They reported that 84% of the variation in feed

consumption could be explained by the independent variables used in the regression equations.

Hagger and Marguerat (1985) stated that body weight raised to the power of either .75 or .50 in place of 1 did not improve the accuracy of predicting feed consumption. They concluded that this result could arise from the almost perfect linearity of transformed values in the body weight range involved. This was in agreement with McDonald (1978).

Variation was considerable in the partial regression of body weight change on feed consumption (Brody, 1945; Leeson et al., 1973; Hagger and Abplanalp, 1978; Hagger and Marguerat, 1985). The statistical relationship between change in body weight and feed consumption in laying hens, according to Hagger and Marguerat (1985), was highly variable and influenced by age of birds, duration of test period, concentration of nutrients in the feed, genetic differences between populations, and other effects. Genetic improvement of the residual feed consumption may become economically significant as gains on egg production tend to a plateau, as pointed out by Bordas and Merat (1981).

### Inheritance of Efficiency

#### General Aspects

Hess et al. (1941) found a high correlation between the efficiency of purebred progeny and crossbred progeny produced by the same sire and concluded that the efficiency of feed utilization is inherited. Hess and Jull (1948) noted that there was a definite inherent difference in efficiency of feed utilization between individuals that could not be

explained on the basis of body weight, rate of gain, or trial differences.

Fox and Bohren (1954) reported significant breed differences in the regression of efficiency on average body weight and postulated that this might be an indication of breed differences in efficiency independent of growth.

Wilson's (1969) study on genetic aspects of feed efficiency for weight gain in broilers suggested that genetic factors, in addition to body weight, may be important. He reported that selection for gain in body weight was only 75% as efficient in improving feed efficiency as direct selection for a low feed/gain conversion ratio.

Bordas and Merat (1981) studied the significance of the residual feed component in two brown-egg strains. Expected feed consumption was estimated from a multiple regression equation using as independent variables metabolic body weight, body weight change during the test period, and egg mass produced during the test period. The residual was then calculated as observed feed consumption minus expected feed consumption. They reported highly significant differences between sire families for the residual in both strains for females.

The practical significance of these regression approaches, from a genetic point of view, hinges on the possible use of the regression coefficients as selection criteria. That is, the regression coefficient for maintenance and for egg mass might be used as selection criteria for separately improving maintenance efficiency and production efficiency. A preliminary step would be to obtain evidence that the differences between the regression coefficients have a genetic basis, for example,

as measured between lines or other genetic groups (Nordskog et al., 1972).

### Heritability and Genetic Correlation

Heritability ( $h^2$ ) is defined as the ratio of additive genetic variance to phenotypic variance (Falconer, 1981). Correlation is a measure of the degree to which variables vary together or a measure of the intensity of association. Genetic correlations are correlations between the additive genetic values.

Harris (1969) reported heritability estimates of .15 to .57 for feed conversion based on sire plus dam component of variance. Wilson (1969) calculated the heritability of feed conversion by regression of offspring on sire to be between .34 to .81 and by regression of offspring on dam to be between .50 to .89 in layers.

Arboleda et al. (1976) estimated the heritability of the residual component of feed consumption, defined as the residual amount of feed consumption after statistical adjustment only for variation in egg mass output and body weight. They found a heritability of .01 and .29 calculated from the sire and from dam component of variance, respectively. Using the same definition of the residual of feed consumption, Wing and Nordskog (1982a) reported heritability values for the residual of feed consumption for two White Leghorn populations of .29 and .15 from the sire component and .21 and .50 from the dam component of variance.

The residual of feed consumption was defined by Hagger and Abplanalp (1978) as feed consumption adjusted for body weight, change in



body weight, egg mass, and age at first egg produced. Heritability estimates of the residual of feed consumption reported by Hagger and Abplanalp (1978) showed decline from the early period (from 20 to 40 weeks of age) to the late period (from 40 to 60 weeks of age). Their estimates calculated from the sire component of variance of three White Leghorn populations were .56, .50, and .64 for the early period and .30, .22, and .64 for the late period.

Bentsen (1982) calculated the heritability of the residual of feed consumption, defined as feed consumption adjusted for metabolic body weight, body weight change, and egg mass output using sire plus dam components of variance of two different breeds. The results of both breeds showed a tendency for lower estimates from older birds in agreement with Hagger and Abplanalp (1978). The heritability estimates were .54 and .51 in the early period (from 16 to 22 weeks of age) and .22 and .00 in the late period (from 34 to 66 weeks of age) for White Leghorn and Rhode Island Red, respectively.

Heritability values between .51 and .59 were reported by Hagger and Marguerat (1985) for the residual of feed consumption calculated from the sire component of variance. They defined the residual as feed consumption adjusted for body weight, change of body weight, egg mass, age at first egg, feathering condition, and egg composition.

The moderately high heritability of the residual component, as estimated, suggests that individual feed consumption records will enhance selection for efficiency of egg production (Wing and Nordskog, 1982a; Hagger and Marguerat, 1985).

Maijala (1966) reported a phenotypic correlation of  $-.51$  and a genetic correlation of  $-.73$  between egg mass and feed conversion in layers. Wilson (1969) reported a phenotypic correlation of  $-.52$  between feed conversion and gain,  $.78$  between gain and feed consumption and  $.07$  between feed conversion and feed consumption in broilers.

## CHAPTER 3 MEASURING ENERGY EFFICIENCY OF INDIVIDUAL LAYING HENS

### Introduction

Because feed accounts for at least two-thirds of the total egg producing cost in high producing birds, even small improvements in feed efficiency would be of economic importance. The most commonly used criterion for measuring egg production efficiency has been feed conversion. Feed conversion (FC) in the laying hen is defined as the ratio of feed input to egg production output. Egg production efficiency also is measured in terms of total feed energy, as the fraction of energy that a hen converts to eggs. Brody (1945) called this ratio gross efficiency (GE).

Feed consumption is determined primarily by the needs of the bird due to egg mass output and body weight maintenance. Breeders, therefore, have relied upon selection for high egg production and low body weight to improve feed efficiency as a correlated response to selection. The breeders have attained a measure of success by the indirect selection methods they have used (Nordskog et al., 1972). However, a limiting factor in this approach is the positive genetic correlation between body weight and egg size, while gains on egg production tend to plateau (Bordas and Merat, 1981).

A more recent way to measure efficiency is the "residual" component of feed consumption. Residual can be defined as the amount of feed

consumption remaining after adjustment for body weight, body weight change and egg mass output. Little information is available concerning correlations among residual food consumption and production traits as well as physiological or morphological traits (Bordas and Merat, 1981).

This experiment was conducted to compare four different methods of measuring energy efficiency of laying hens.

### Experimental Procedure

One hundred and four individually caged DeKalb DK hens, 44 weeks of age, were used in this experiment. They were maintained in individual cages and were given a corn-soybean meal diet formulated to meet their daily nutritional requirements as suggested by Harms (1981). The diet was calculated to contained 15.5% protein and 2890 kcal ME/kg. Each cage was equipped with two individual feed cups as described by Roland *et al.* (1971), providing sufficient feed for 1 week. Hens were weighed individually at the beginning of the experiment and at the end of each week for 3 weeks. These weights were used to calculate average body weight (BW) and average daily change in body weight (BC) during each weekly period as well as for the 3-week period.

Egg production was recorded daily. All eggs were weighed daily for the experimental period. Egg production and egg weight were used to calculate average daily egg mass (EM) for each weekly period and for the 3-week period. The feed was weighed at the beginning and end of each weekly period. Metabolizable energy intake (MEI) was calculated by multiplying feed intake by metabolizable energy content of the diet.

Duncan's multiple range test (Duncan, 1955) was used to compare weekly means of MEI, BW, BC, and EM.

A multiple regression equation was developed describing the relationship between MEI and metabolic body weight ( $BW^{.75}$ ), BC, and EM. The mathematical model used was

$$MEI = b_1 BW^{.75} + b_2 BC + b_3 EM + RES$$

where MEI, BW, BC and EM are average values for the 3-week-period.

$b_1$  = the partial regression of MEI intake on  $BW^{.75}$ .

$b_2$  = the partial regression of MEI intake on BC.

$b_3$  = the partial regression of MEI intake on EM.

RES = the residual component.

The partial regression coefficients were used to estimate the expected metabolizable energy (ExME) using the model:

$$ExME = b_1 BW^{.75} + b_2 BC + b_3 EM$$

Both FC and GE were calculated for each hen. The partial regression coefficient of MEI on EM ( $b_3$ ) was used to estimate energy required for egg production and subsequently to calculate GE. The relative efficiency ratio (RER), defined as:  $ExME/MEI \times 100$ , also was calculated for each hen.

### Results and Discussion

The MEI was significantly lower in the first week than the second and the third weeks (Table 3-1). Neither BW nor the EM changed significantly during the experimental period, although BW did vary among weeks.

For every 2.06 grams of feed intake 1 gram of egg was produced (Table 3-2). Only 23.7% of the total energy intake was used for egg production. Joshi et al. (1949) reported that in New Hampshire hens 27% of the feed consumed was used for the production of eggs.

In all the available studies on the residual as a measurement of efficiency, feed consumption was the dependent variable. Poultry tend to eat to satisfy their energy requirements if fed ad libitum (NRC, 1984). Dietary energy, protein, density, and volume all have significant effects upon feed consumption (Gleaves et al., 1968). After reviewing the data from 34 published reports, Morris (1968) observed that groups of hens offered diets with different energy levels tend to adjust consumption so as to maintain a similar caloric intake. It is generally recognized among poultry nutritionists that a primary determinant of feed intake is the energy concentration of the diet (Pesti, 1982; Pesti and Fletcher, 1983).

The multiple regression equation describing the relationship between  $BW^{.75}$ , BC, and EM and MEI was

$$ExME = (0.930 \pm .045) BW^{.75} + (3.484 \pm .891) BC + (1.383 \pm .218) EM$$

Table 3-1. Means and standard errors for metabolizable energy intake (MEI), body weight (BW), body weight change (BC), and egg mass (EM).

	MEI	BW	BC	EM
First week	289.31 b <u>+3.46</u>	1563.63 a <u>+14.68</u>	-2.16 b <u>+.61</u>	50.33 a <u>+1.02</u>
Second week	306.68 a <u>+3.63</u>	1568.46 a <u>+14.64</u>	3.55 a <u>+.49</u>	50.11 a <u>+1.19</u>
Third week	306.51 a <u>+3.42</u>	1574.02 a <u>+14.86</u>	-1.95 b <u>+.54</u>	51.20 a <u>+1.14</u>
<hr/>				
Three-week	300.83 <u>+3.10</u>	1568.74 <u>+14.68</u>	-0.19 <u>+.23</u>	50.55 <u>+0.94</u>

Figures in the same column followed by a common letter do not differ significantly ( $p < 0.05$ ).

Table 3-2. Means and standard errors of feed conversion (FC), gross efficiency (GE), the residual (RES), and the relative efficiency ratio (RER).

	Means and Standard Errors	Equation for estimate
FC	2.06 $\pm$ 0.03	$\frac{\text{Feed intake}}{\text{EM}}$
GE %	23.71 $\pm$ 0.28	$\frac{(\text{EM} * b_3) * 100}{\text{MEI}}$
RES	00.00 $\pm$ 2.11	MEI - ExME
RER %	100.00 $\pm$ 0.71	$\frac{\text{ExME} * 100}{\text{MEI}}$

EM = egg mass

$b_3$  = the partial regression coefficient of MEI on EM

MEI = metabolizable energy intake

ExME= expected metabolizable energy



The partial regression coefficients of MEI on metabolic BW, BC, and EM were significant ( $p < .0001$ ).

A correlation of  $-.68$  was found between FC and EM and  $.64$  between GE and EM (Table 3-3). The high correlation between EM and both FC and GE reflects the fact that these two efficiency measurements are biased for high egg mass output. Koch et al. (1963), in a study of feed conversion (FC) in beef cattle, pointed out that efficiency is not a directly measurable trait. These workers suggested abandoning the use of a ratio to express feed efficiency on the grounds that ratio is a biased estimate, because of the automatic relationship which occurs simultaneously among the three variables, gain, feed consumption and efficiency. Instead of using FC ratio for measuring feed efficiency, they proposed the deviation between actual gain and expected gain calculated from a regression equation with feed consumed as the independent variable.

Hens consume feed primarily to meet their energy requirements (Scott et al., 1976). Because energy required for production can be estimated from egg mass and body weight gain and that required for maintenance can be estimated from body weight, the energy in feed consumed not converted to egg or body gain, or not expended for body maintenance would represent the residual component. The variation among individual hens in RES reflects the variation in efficiency of digestion and metabolism. Another component of RES is feed wastage. Bordas and Merat (1981) and Wing and Nordskog (1982a) reported that the RES was heritable. This finding suggests that there is a genetic basis for

Table 3-3. Correlations and level of significance among egg production efficiency measurements and economic traits.

	BW	BC	EM	MEI	FC	GE	RES
BC	.026 .80						
EM	.369 .00	.014 .89					
MEI	.622 .00	.239 .02	.514 .00				
FC	.101 .31	.200 .04	-.684 .00	.184 .06			
GE	-.151 .13	-.202 .04	.644 .00	-.319 .00	-.932 .00		
RES	-.025 .80	-.038 .70	.037 .72	.675 .00	.408 .00	.548 .00	
RER	.010 .92	.029 .77	-.046 .65	-.681 .00	-.414 .00	.555 .00	-.991 .00

BW = body weight  
 BC = body weight change  
 EM = egg mass  
 MEI = metabolizable energy intake  
 FC = feed conversion  
 GE = gross efficiency  
 RES = residual component of MEI  
 RER = relative efficiency ratio

individual differences of the feed residual associated with digestion and metabolism and or a psychogenetic basis of feed efficiency.

The high correlation between RES and RER suggests that these measurements, to some extent, are equivalent. Both RES and RER are significantly correlated to FC and GE. There were no correlations between either RES or RER and any of the production traits (BW, BC, and EM), since both RES and RER were adjusted for the production traits.

These data indicated that a considerable difference in any of the egg production efficiency measurements used (FC, GE, RES, and RER) can be detected between individual hens within a flock. It is suggested that these measurements of egg production efficiency may have potential to be used as selection criteria for improving feed efficiency. A preliminary step would be to obtain evidence that the variability in these measurements has a genetic basis, for example, as measured between lines or other genetic groups.

CHAPTER 4  
A COMPARISON OF ENERGY EFFICIENCY OF  
SIX WHITE LEGHORN LINES

Introduction

Genetic improvement of egg-type chickens for high production efficiency has had a long and successful history based on selection for high rates of egg laying. In some instances, however, commercial breeders have attempted to select for reduction in body size as a means of further lowering the feed required per egg laid. Increases in average egg size also may contribute to more efficient production of eggs. This genetic improvement, however, may have limits; hence it is of interest to consider that part of the variability in feed intake which is independent of egg production and body size (Bordas and Merat, 1981). The unexplained variation in efficiency can be thought of as variation in deviations between observed and expected feed consumption or metabolizable energy intake when egg production, body weight change, and body weight are taken into consideration. The expected metabolizable energy can be estimated from multiple regression with metabolizable energy intake as the dependent variable and metabolic body weight, body weight change, and egg mass as independent variables (Bordas and Merat, 1981).

The practical significance of these regression approaches, from a genetic point of view, hinges on the possible use of the regression coefficients as selection criteria. A preliminary approach would be to

obtain evidence that the differences between the regression coefficients have a genetic basis, for example, as measured between lines or other genetic groups (Nordskog et al., 1972).

This experiment was designed to examine the differences among the partial regression coefficients (b's) values for maintenance, body weight change, and egg mass output of six genetic lines of White Leghorn.

#### Experimental Procedure

One hundred and eighty hens from six different white-Leghorn-type<sup>1</sup> genetic lines (30 hens/line) were used in this study. The experimental diet contained 2825 kcal of metabolizable energy and 164.5 g protein per kg. The hens were caged individually in three rows. They were randomly distributed so that each row had 10 hens of each line. Each hen was provided with two 946 ml plastic containers used as feed cups. The plastic containers were prepared as described by Roland et al. (1971). Each hen was weighed at the beginning of the study and then weekly for 4 weeks. The weights were used to calculate average body weight (BW) and average body change (BC), as grams per day, during the experimental period. Total feed consumption was recorded weekly for each hen and was used to calculate metabolizable energy intake (MEI). Egg production and egg weight were recorded daily in order to calculate egg mass (EM), as grams per day, for each hen.

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<sup>1</sup> The birds were provided by Hy-Line International. West Des Moines, Iowa.

A multiple regression equation was developed describing the relationship between MEI and metabolic body weight ( $BW^{.75}$ ), BC, and EM. The mathematical model used was

$$MEI = b_1 BW^{.75} + b_2 BC + b_3 EM + RES$$

where  $b_1$  = the partial regression of MEI on  $BW^{.75}$

$b_2$  = the partial regression of MEI on BC

$b_3$  = the partial regression of MEI on EM

RES = the residual component.

This model was used to develop an equation for each line as well as an overall equation using the six-lines data pooled together. The expected metabolizable energy (ExME) was calculated two times for each hen, by using the partial regression coefficients of the equation of its line and by using those coefficients of the overall equation. The model used was:

$$ExME = b_1 BW^{.75} + b_2 BC + b_3 EM$$

The correlation between the two estimates of ExME was calculated within lines.

The residual component of energy intake (RES) (defined as the difference between the MEI and the ExME) and the relative efficiency ratio (RER) (defined as  $ExME / MEI \times 100$ ) were calculated for each hen using the partial regression coefficients of the overall equation. Feed

conversion (FC) (the ratio of feed consumed to EM) also was calculated for each hen.

Duncan's multiple range test (Duncan, 1955) was used to compare means of MEI, BW, BC, EM, and FC among the lines. The least significant difference multiple comparison test was used to compare the partial regression coefficients for BW<sup>.75</sup>, BC, and EM of the six-lines (Steel and Torrie, 1980).

### Results and Discussion

The six lines differed significantly ( $P < 0.05$ ) in their MEI, BW, BC, and EM (Table 4-1). The MEI ranged from 265 kcal/day for L-2 to 342 kcal/day for L-5; BW ranged from 1445 g for L-2 to 1723 g for L-1; BC ranged from -1.75 g/day for L-3 to 1.17 g/day for L-2; and EM ranged from 36.4 g/day for L-6 to 53.3 g/day for L-1.

The most commonly used criterion for measuring efficiency has been FC or its reciprocal. High correlations were found between FC and EM (Table 4-2). The correlation between FC and EM ranged from -.69 for L-2 to -.94 for L-3. Maijala (1966) reported a phenotypic correlation of -.51 and a genetic correlation of -.73 between EM and FC.

Using FC as selection criterion for improving feed efficiency will require individual feed consumption records, which is a costly procedure. Because of the high correlations between production (either body weight gains as in meat animals or egg mass for layers) and FC, breeders usually assume that only the production is worth measuring and that selection based on production will give a high correlated response in FC (Nordskog et al., 1972). However, Siegel and Wisman (1966), after

Table 4-1. Means and standard errors for metabolizable energy intake (MEI), body weight (BW), body weight change (BC), and egg mass (EM) for six White Leghorn lines.

Line	MEI	BW	BC	EM
L-1	331.65 ab ± 5.11	1723.70 a ± 19.58	-0.78 cd ± .41	53.27 a ± 1.37
L-2	265.31 d ± 4.03	1445.10 d ± 19.03	1.17 a ± .34	39.60 cd ± .63
L-3	281.31 c ± 6.47	1563.53 c ± 24.67	-1.75 d ± .39	41.58 bcd ± 2.43
L-4	315.89 b ± 4.45	1620.30 bc ± 16.44	-0.03 abc ± .39	45.14 b ± 1.61
L-5	342.36 a ± 6.53	1670.87 ab ± 25.30	-0.13 bc ± .53	42.27 bc ± 2.61
L-6	326.51 ab ± 5.80	1575.13 c ± 21.45	0.72 ab ± .42	36.64 d ± 1.29

Figures in the same column followed by a common letter do not differ significantly ( $P < 0.05$ )

Table 4-2. Correlations between feed conversion (FC) and egg mass (EM)

L-1	L-2	L-3	L-4	L-5	L-6
-.817	-.685	-.946	-.922	-.882	-.859

Note: All correlations were significant ( $p < .0001$ ).



five generations of selection for high and low body gain at 8 weeks of age in White Plymouth Rocks, observed no differences between the two selected lines in feed conversion. They concluded that selection for increased body weight, when feed was provided ad libitum, was largely a selection for appetite.

In order to compare energy utilization efficiency among the six genetic lines using the residual component of metabolizable energy intake (RES), the data of the six-lines were pooled and an overall multiple regression equation was developed describing the relationship between MEI and  $BW^{.75}$ , BC, and EM. The equation derived was as follows:

$$MEI = (1.083 \pm .036) BW^{.75} + (5.915 \pm .861) BC + (0.875 \pm .207) EM + RES$$

The partial regression coefficients of MEI on metabolic BW, BC, and EM were significant ( $p < .0001$ ).

Using the partial regression coefficients of the above equation the residual components of energy intake (RES) and the relative efficiency ratio (RER) were calculated for each hen. There were significant differences among the lines in efficiency regardless of efficiency measurement used (Table 4-3). Using the FC as the criterion for measuring efficiency showed that L-1, L-2, L-3, and L-4 were not significantly different. The lower MEI (Table 4-1) and the high efficiency measured as FC showed by L-2 (Table 4-2) were in part due to lower body maintenance required for that line since this line had the lowest body weight. The total energy required for maintenance varies directly with the body weight of an animal although metabolic rate, per

Table 4-3. Means and standard errors of the residual component (RES), the relative efficiency ratio (RER), and feed conversion (FC) for six White Leghorn lines

Line	RES	RER	FC
L-1	$-.05 \pm 4.41$	$100.35 \pm 1.33$	$2.23 \pm .05$ b
L-2	$-30.05 \pm 2.59$	$111.59 \pm 1.06$	$2.39 \pm .05$ b
L-3	$-13.90 \pm 3.22$	$105.64 \pm 1.42$	$2.53 \pm .15$ b
L-4	$-.05 \pm 3.43$	$100.33 \pm 1.10$	$2.60 \pm .13$ b
L-5	$23.15 \pm 4.50$	$93.61 \pm 1.26$	$3.70 \pm .53$ a
L-6	$19.47 \pm 4.69$	$94.57 \pm 1.34$	$3.32 \pm .18$ a

Figures in the FC column followed by a common letter do not differ significantly ( $P < 0.05$ ).

unit of body weight, varies inversely with body weight. The net result is that total maintenance requirement is greater in large than in small birds (Mellen, 1963).

Hens consumed feed primarily to meet energy requirements for maintenance, body weight gain, and egg production. A multiple regression equation was developed for each genetic line to compare energy utilization for maintenance and for egg production among the lines (Table 4-4).

Significant differences between the partial regression coefficients for maintenance were detected among the lines. The difference in energy requirement for maintenance among different genetic lines could be explained in part as a difference in activity. Estimation of energy losses resulting from activity are difficult to predict. Evidence indicates that activity heat losses associated with eating and with the mechanical process of egg production in the oviduct are small (van Kampen, 1976). Another possible source of variation in maintenance requirements among the lines was feathering condition. In our study, however, neither volunteer activity nor feathering condition were examined and were considered as parts of the genetic differences among the lines. Farrell (1975) observed significant differences in maintenance energy requirements of White Leghorn, Australorp and crossbred (WL x Ao) hens. Using Rhode Island Red and White Leghorn breeds Bentsen (1982) also found significant differences in the partial regression coefficients for maintenance.

The partial regression coefficient for BC of L-6 was significantly larger ( $P > 0.05$ ) than those for L-1, L-3, L-4, and L-5 (Table 4-4).

Table 4-4. Partial regression coefficients, standard errors, and levels of significance for six White Leghorn lines.

Line	BW-75		BC		EM	
L-1	0.879 + 0.142 0.0001	bc	2.784 + 2.064 0.1792	b	1.846 + 0.689 0.0082	a
L-2	1.030 + 0.186 0.0001	abc	6.761 + 2.107 0.0016	ab	0.403 + 1.082 0.7702	a
L-3	0.842 + 0.058 0.0001	c	3.197 + 1.819 0.0807	b	1.865 + 0.312 0.0001	a
L-4	1.021 + 0.085 0.0001	bc	2.735 + 1.881 0.1479	b	1.226 + 0.473 0.0705	a
L-5	1.212 + 0.047 0.0001	a	6.450 + 1.319 0.0001	b	0.621 + 0.273 0.0243	a
L-6	1.077 + 0.083 0.0001	ab	10.808 + 1.688 0.0001	a	1.342 + 0.557 0.0771	a

Figures in the same column followed by a common letter do not differ significantly ( $P < 0.05$ ).

Table 4-5. Correlation coefficients between the two expected metabolizable energy (ExME) intakes estimated for each hen calculated separately for each line.

L-1	L-2	L-3	L-4	L-5	L-6
.968	.992	.941	.891	.992	.947

Note: ExME estimated using the overall equation, as well as using the equation derived for each line.

All correlations were significant ( $p < .0001$ ).

During the experimental period L-6 gained weight while L-1, L-3, L-4, and L-5 lost weight (Table 4-1). In the statistical analysis it was assumed that energy required for a gram of body gain is equal to energy utilized by a gram of body loss. This assumption was not very accurate. Results suggested that body gain and body loss should be considered two different characteristics. Body weight gain in mature hens is most likely deposited fat; however, body loss in high producing hens could be muscular tissues.

No significant differences were found among the partial regression coefficients of MEI on EM of the six-lines (Table 4-4). Bentsen (1982) found no differences between the partial regression coefficients of feed intake on EM of Rhode Island Red and White Leghorn. Leeson et al. (1973) published two multiple regression equations based on observations of two breeds of hens. Differences in coefficients for both metabolic body weight and egg mass of the two equations indicated differences between the two breeds in their efficiency for maintenance and egg production.

Several regression equations have been developed by using body weight or body weight raised to a power between .5 and .75, body weight change, and egg mass to predict the daily intake of feed (or metabolizable energy) of laying hens. McDonald (1978) reviewed data used for some of these equations and concluded that many factors were influencing the accuracy of the prediction by the equations. These were assumptions and methodology, seasonal effects, housing effects, management, nutrition, and genetics.

The correlation between ExME estimated using the b values of the overall equation, which was derived using the data of the six-lines pooled together and ExME estimated using the b values of the equations developed for each line (table 4-5), ranged from 0.891 for L-4 to 0.992 for L-2 and L-5. However, using the overall equation to predict metabolizable energy required for the six-lines (Table 4-3) resulted in over-estimation of up to 11.59% for L-2 (RER = 111.59%) and under-estimation of up to 6.39% for L-5 (RER = 93.61%). Results showed that high correlation between ExME calculated using different equations do not guarantee the accuracy of the metabolizable energy prediction. Leeson et al. (1973) stated that multiple regression equations were limited in their capability of prediction.

Results of this study suggested that more consideration should be given to differences among various genetic stocks in their requirement for maintenance and egg production and the possible use of partial regression coefficients as selection criteria for separately improving maintenance efficiency and egg production efficiency.

CHAPTER 5  
MEASURING GENETIC VARIATION IN METABOLIZABLE ENERGY INTAKE OF  
LAYING HENS ADJUSTED FOR BODY WEIGHT AND EGG PRODUCTION

Introduction

Since feed accounts for at least two-thirds of the total costs of producing eggs, any improvement in efficiency of feed utilization is important. Efficiency of feed conversion by laying hens depends on their egg production and body weight and it has been improved considerably by breeding to increase the former and to decrease the latter. This genetic improvement may have limits. More attention now is given to that part of the variability in feed intake which is independent of egg production and body size or the residual component of feed consumption. The residual can be defined as feed consumption statistically adjusted for body weight, body weight change, and egg mass output.

Heritability estimates of the residual component of feed consumption ranged between zero (Arboleda et al., 1976; Bentsen, 1982) to 0.5 or higher (Hagger and Abplanalp, 1978; Bentsen, 1982; Hagger and Marguerat, 1985). This wide range of heritability estimates not only reflects genetic differences between breeds and flocks used but also differences in techniques used in estimation. The test period ranged from 4-week period (Arboleda et al., 1976) to 50-week period (Bentsen, 1982). Some studies used partial measurements for estimating egg mass

output (Arboleda et al, 1976; Wing and Nordskog, 1982a; Hagger and Marguerat, 1985). Adjustment for change in body weight was not considered by some workers (Arboleda et al, 1976; Wing and Nordskog, 1982a).

Measuring the residual component of feed consumption is a costly and time consuming procedure, since it requires records on feed consumption, body weight, egg production, and egg weight for a certain period of time, on an individual bird basis. In this investigation, the effects of the test period length, egg mass output, and age were examined in order to find the shortest test period which could be used to measure the residual and its heritability.

#### Experimental Procedure

Three hundred and thirty five pedigreed White Leghorn type layers<sup>1</sup> were used in this study. At 22 weeks of age, pullets were randomly assigned to three adjoining rows, each row having 140 individual (20 x 45 x 40 cm) cages. The cages in each row were arranged in double-deck stair-step system. Each hen was provided with two plastic containers used as feed cups. The plastic cups were prepared as described by Roland et al. (1971). Light was provided 16 h per day during the experiment. The experiment started when the hens reached 26 weeks of age and lasted for 28 weeks. The diet used during the first 24 weeks contained 18.5% protein and 2870 kcal me/kg. The diet used during the

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<sup>1</sup> The birds were provided by Hy-Line International. West Des Moines, Iowa.



last 4 weeks of the experiment contained 18% protein and 3037 kcal me/kg.

The birds were weighed at the beginning of the experiment, biweekly up to week 24 (12 2-week periods), and at the end of the study (1 4-week period). These weights were used to calculate average body weights and average daily changes in body weight for each period studied. Egg production and egg weight were recorded daily. Egg production and egg weights were used to calculate average daily egg masses for each period. Feed consumption was recorded weekly for each hen and was used to calculate the average feed consumption per day for each period. The metabolizable energy intake was calculated by multiplying feed consumption by metabolizable energy content of the diet.

To minimize effects of feed and water consumed on body weight measurements and consequently on body weight change, hens as well as feed were weighed around the middle of the 16-h lighting time. At the time of measuring body weight and feed consumption it was assumed that feeding and drinking activities were at their lowest level (Mongin and Sauveur, 1974) and that about 80% of the eggs had already been laid. This minimized effects of the presence of an egg on body weight measurements.

Although yolk development goes through three phases, most of its components are deposited within the final phase, which lasts between 7 to 8 days (Bell and Freeman, 1971). The egg albumen and the shell then are deposited around the mature yolk as it traverses the oviduct. A minimum of 24 to 26 h are required between the time of ovulation and the end of egg shell formation. All these factors add to the difficulty of

measuring egg mass output for a short time period. Three ways of measuring egg mass output were examined: measuring egg mass output starting the same day as measurements of body weight and feed consumption (E0); measuring egg mass starting 2 days after measurements of body weight and feed consumption (E2); and measuring egg mass starting 4 days after measurement of body weight and feed consumption (E4).

The analysis of data from each period was performed in two stages. In the first stage a reduced model was employed. The reduced model was the following multiple regression model:

$$\begin{aligned} \text{MEI} = & u + b_1 (\text{BW} \cdot 75 - \overline{\text{BW}} \cdot 75) + b_2 (\text{BC} - \overline{\text{BC}}) \\ & + b_3 (\text{EM} - \overline{\text{EM}}) + \text{RES} \end{aligned}$$

where:

MEI = metabolizable energy intake.

u = population mean.

BW.75 = metabolic body weight.

BC = body weight change.

EM = egg mass.

b<sub>1</sub> = the partial regression coefficient of MEI on BW.75.

b<sub>2</sub> = the partial regression coefficient of MEI on BC.

b<sub>3</sub> = the partial regression coefficient of MEI on EM.

RES = the residual component of MEI.

A second analysis of data from each period was performed, using a complete model, in order to estimate genetic components of variance.

From analysis of covariance, metabolizable energy intake for each period was adjusted for metabolic body weight, change in body weight, and egg mass output. The mathematical model used was

$$\begin{aligned} MEI_{ijk} = & u + S_i + D_{ij} + b_1 (BW^{.75}_{ijk} - \overline{BW}) + b_2 (BC_{ijk} - \overline{BC}) \\ & + b_3 (EM_{ijk} - \overline{EM}) + e_{ijk} \end{aligned}$$

where:

$MEI_{ijk}$  = metabolizable energy intake per day of the kth progeny from the jth dam mated to the ith sire.

$u$  = population mean.

$S_i$  = random effect of the ith sire.

$D_{ij}$  = random effect of the jth dam mated to the ith sire.

$BW^{.75}_{ijk}$  = metabolic body weight of the kth progeny from the jth dam mated to the ith sire.

$BC_{ijk}$  = body weight change of the kth progeny from the jth dam mated to the ith sire.

$EM_{ijk}$  = the egg mass produced per day of the kth progeny from the jth dam mated to the ith sire.

$b_1$  = the partial regression coefficient of MEI on  $BW^{.75}$ .

$b_2$  = the partial regression coefficient of MEI on BC.

$b_3$  = the partial regression coefficient of MEI on EM

$e_{ijk}$  = random error component.

A multiple regression equation was developed for each hen using 2-week period data available for that hen. The mathematical model was

$$MEI = b_1 BW + b_2 BC + b_3 EM + e$$

where:

$b_1$ ,  $b_2$ , and  $b_3$  = the partial regression coefficients of MEI on  
body weight, change in body weight, and egg mass.  
 $e$  = the random error component.

From the partial regression coefficients of MEI on body weight and egg mass two sets of data were established. Only significant partial regression coefficients ( $p < .05$ ) were considered. Genetic components of variance were estimated for partial regression coefficients of MEI on BW (289 observations) and EM (215 observations) using the following model:

$$b_{ijk} = u + S_i + D_{ij} + e_{ijk}$$

where:

$b_{ijk}$  = partial regression coefficient of MEI on BW (or EM)  
of the  $k$ th progeny of the  $j$ th dam mated to the  $i$ th  
sire.

$u$  = population mean.

$S_i$  = random effect of the  $i$ th sire.

$D_{ij}$  = random effect of the  $j$ th dam mated to the  $i$ th sire.

$e_{ijk}$  = random error component.

Heritabilities were estimated for the residual and for the partial regression coefficients of MEI on BW and EM. For estimating the heritability, the variance components, the mean squares for sire, dam,

and error were equated to their expectations following Henderson (1953).

The estimate of heritability was derived:

$$h^2_{S+D} = 2( S + D ) / ( S + D + E )$$

where:

$h^2_{S+D}$  = heritability estimate from sire plus dam components of variance.

S, D, and E = sire, dam, and error components of variance.

### Results and Discussion

The number of birds with complete records, means, standard errors for metabolizable energy intake, body weight, body weight change, and egg mass for all periods are presented in Table 5-1. Egg mass peaked within 32 and 38 weeks of age, and declined thereafter due primarily to a decline in egg number, while body weight increased about 100 g during the 28-week experimental period.

The coefficient of determination ( $R^2$ ) was used to examine the different egg mass measurements used (Table 5-2). The coefficient of determination represents the fraction of the total variation in the energy intake explained by the model. Using E2 improved the fitness of the model by about 2.5% compared to E0 and E4. Most yolk components are deposited within the last 7 to 8 days before ovulation (Bell and Freeman, 1971). The protein of the albumen secreted around the yolk as it passes down the magnum is already present before the secretory process is initiated (Oshima and Nozaki, 1960). Shell formation requires about 20 h (Bell and Freeman, 1971). Thus any feed consumed by

Table 5-1. Number of birds, means, and standard errors for metabolizable energy intake (MEI), body weight (BW), change in body weight (BC), and egg mass output (EM).

Age	#	MEI	BW	BC	EM
26-28	335	267.70 $\pm$ 1.92	1354.70 $\pm$ 4.90	-.31 $\pm$ .19	38.73 $\pm$ .57
28-30	331	258.13 $\pm$ 1.64	1359.69 $\pm$ 4.97	.88 $\pm$ .16	39.89 $\pm$ .49
30-32	321	269.86 $\pm$ 1.64	1365.29 $\pm$ 5.14	-.06 $\pm$ .16	41.28 $\pm$ .46
32-34	320	273.15 $\pm$ 1.61	1374.60 $\pm$ 5.39	1.34 $\pm$ .14	41.76 $\pm$ .42
34-36	316	278.56 $\pm$ 1.62	1392.14 $\pm$ 5.72	1.35 $\pm$ .13	42.30 $\pm$ .42
36-38	305	274.88 $\pm$ 1.71	1399.75 $\pm$ 6.19	-.19 $\pm$ .15	41.28 $\pm$ .44
38-40	301	269.33 $\pm$ 2.06	1396.06 $\pm$ 6.71	-.50 $\pm$ .17	40.68 $\pm$ .46
40-42	304	279.96 $\pm$ 1.80	1402.15 $\pm$ 6.94	1.52 $\pm$ .15	40.30 $\pm$ .48
42-44	308	262.47 $\pm$ 1.61	1411.28 $\pm$ 7.05	.16 $\pm$ .15	39.85 $\pm$ .46
44-46	318	271.84 $\pm$ 1.61	1414.09 $\pm$ 7.28	1.36 $\pm$ .15	39.86 $\pm$ .42
46-48	315	248.16 $\pm$ 1.63	1416.62 $\pm$ 7.73	-.76 $\pm$ .16	37.59 $\pm$ .45
48-50	313	254.29 $\pm$ 1.74	1423.95 $\pm$ 8.30	1.89 $\pm$ .16	36.98 $\pm$ .44
50-54	319	259.19 $\pm$ 1.81	1455.24 $\pm$ 9.12	1.73 $\pm$ .11	34.80 $\pm$ .44

Table 5-2. Effect of different egg mass measurements on coefficients of determination of the reduced model.

Age	E0 <sup>1</sup>	E2 <sup>1</sup>	E4 <sup>1</sup>
26-28	.554	.588	.567
28-30	.639	.648	.630
30-32	.565	.623	.581
32-34	.595	.616	.588
34-36	.583	.610	.588
36-38	.609	.623	.615
38-40	.643	.672	.643
40-42	.623	.629	.605
42-44	.600	.633	.596
44-46	.575	.609	.580
46-48	.649	.645	.611
48-50	.651	.659	.629
Means	.607	.629	.603

<sup>1</sup> E0 measuring egg mass output starting the same days of measuring body weight and feed consumption.

E2, E4 measuring egg mass output starting 2 days or 4 days after measuring body weight and feed consumption, respectively.

Note: See text for description of the reduced model.

a hen within a day will not contribute much to the yolk or the albumen of an egg produced on that day. In all the following only E2 was calculated and referred to as egg mass output (EM).

Coefficients of determination or  $R^2$  for the reduced and complete models are presented in Table 5-3. The difference between the  $R^2$  values of the reduced and complete model represent the fraction of the total variation in metabolizable energy intake explained by the independent variables added to the model, in addition to the effects of metabolic body weight, the change in body weight, and egg mass output.

Measuring the residual component of feed consumption is costly and time consuming. However, moderately high heritability of the residual implies that genetic gain in efficiency can be enhanced by using information on the residual component of feed consumption in breeding programs. Genetic improvement of the residual is becoming more significant as gains in egg production tend to a plateau. Reducing the cost of measurements can be achieved by shortening the period of collecting data.

Effects of length of test period on coefficients of determination for the reduced and complete models are presented in Table 5-3. Although the 8-week period showed higher  $R^2$  values, more improvement was gained by using 4-week period compared to 2-week period than the improvement gained by using 8-week period compared to a 4-week period. This improvement is more obvious from the coefficient of determination calculated from the reduced model where it was, on the average, .629, .691 and .720 for the 2-week, 4-week, and 8-week periods, respectively.



Table 5-3. Coefficients of determination from reduced (R) and complete model (C).

2-Week			4-Week			8-Week		
Age	R	C	Age	R	C	Age	R	C
26-28	.588	.870	26-30	.680	.903	26-34	.704	.908
28-30	.648	.898	28-32	.691	.899	28-36	.716	.918
30-32	.623	.869	30-34	.679	.902	30-38	.718	.936
32-34	.616	.897	32-36	.657	.907	32-40	.711	.946
34-36	.610	.889	34-38	.670	.928	34-42	.703	.945
36-38	.623	.911	36-40	.698	.946	36-44	.734	.954
38-40	.672	.926	38-42	.696	.939	38-46	.691	.944
40-42	.629	.925	40-44	.692	.933	40-48	.718	.937
42-44	.633	.907	42-46	.651	.922	42-50	.733	.941
44-46	.609	.897	44-48	.696	.919	46-54	.773	.933
46-48	.645	.900	46-50	.715	.921			
48-50	.659	.880	50-54	.771	.927			
Means	.629	.897		.691	.921		.720	.936

Note: See text for description of reduced and complete models.

The partial regression coefficients of metabolizable energy intake on metabolic body weight declined with age regardless of test period length used (Table 5-4). Leeson et al. (1973) reported a gradual decrease in the  $W^{.75}$  factor with age in the two commercial type layers used. Hagger and Abplanalp (1978) reported a decline in the magnitude of the partial regression coefficients of food consumption on body weight from the early period (from 20 to 40 weeks of age) to the later period (from 40 to 60 weeks of age) in the three populations of White Leghorn studied. Another factor in our experiment which contributed to the reduction of energy required for maintenance was that the experiment started in the winter (January) and ended in the summer (July).

The partial regression coefficients of metabolizable energy intake on body weight change, on the average increased from 2.49 for 2-week to 3.87 for 4-week and 5.15 for 8-week test periods (Table 5-5). The statistical relationship between change in body weight and feed consumption in laying hens, according to Hagger and Marguerat (1985), was highly variable and influenced by age of birds, duration of test period, concentration of nutrients in the feed, genetic differences between populations, and other effects.

The partial regression coefficients of metabolizable energy intake on egg mass output showed a slight increase with age (Table 5-6). Leeson et al. (1973) reported a gradual increase in the partial regression coefficient of egg mass output in one of the two commercial type layers studied. Hagger and Abplanalp (1978) observed increases in the partial regression coefficient of egg mass with age in two of the three White Leghorn populations studied.

Table 5-4. Partial regression coefficients of metabolic body weight (BW<sup>.75</sup>) on metabolizable energy intake (MEI) using 2-week, 4-week, and 8-week periods.

2-Week		4-Week		8-Week	
Age	BW <sup>.75</sup>	Age	BW <sup>.75</sup>	Age	BW <sup>.75</sup>
26-28	1.067 ± .257	26-30	1.118 ± .199	26-34	1.019 ± .169
28-30	.994 ± .195	28-32	.816 ± .180	28-36	.688 ± .159
30-32	.897 ± .220	30-34	.933 ± .179	30-38	.721 ± .155
32-34	1.158 ± .177	32-36	.920 ± .164	32-40	.760 ± .145
34-36	.860 ± .175	34-38	.854 ± .146	34-42	.853 ± .132
36-38	.712 ± .170	36-40	.711 ± .144	36-44	.717 ± .125
38-40	1.057 ± .160	38-42	1.028 ± .129	38-46	.808 ± .116
40-42	.852 ± .130	40-44	.687 ± .107	40-48	.668 ± .107
42-44	.491 ± .135	42-46	.469 ± .121	42-50	.486 ± .113
44-46	.469 ± .129	44-48	.625 ± .116	46-54	.470 ± .109
46-48	.586 ± .129	46-50	.530 ± .116		
48-50	.566 ± .148	50-54	.571 ± .110		
Means	.809 .169	.772 .143		.719 .133	

Table 5-5. Partial regression coefficients of body change (BC) on metabolizable energy intake (MEI) using 2-week, 4-week, and 8-week periods.

2-Week		4-Week		8-Week	
Age	BC	Age	BC	Age	BC
26-28	2.440 $\pm$ .574	26-30	4.773 $\pm$ .851	26-34	5.461 $\pm$ 1.099
28-30	3.824 $\pm$ .561	28-32	5.473 $\pm$ .867	28-36	9.004 $\pm$ 1.334
30-32	3.189 $\pm$ .606	30-34	5.347 $\pm$ .910	30-38	7.782 $\pm$ 1.276
32-34	3.187 $\pm$ .588	32-36	4.850 $\pm$ 1.123	32-40	5.613 $\pm$ 1.249
34-36	1.990 $\pm$ .715	34-38	3.066 $\pm$ .858	34-42	4.626 $\pm$ 1.466
36-38	2.771 $\pm$ .575	36-40	4.304 $\pm$ .711	36-44	5.525 $\pm$ 1.246
38-40	2.149 $\pm$ .562	38-42	2.194 $\pm$ .939	38-46	0.925 $\pm$ 1.320
40-42	1.698 $\pm$ .571	40-44	3.051 $\pm$ .929	40-48	1.895 $\pm$ 1.413
42-44	3.082 $\pm$ .731	42-46	2.437 $\pm$ 1.021	42-50	4.419 $\pm$ 1.430
44-46	1.035 $\pm$ .575	44-48	1.819 $\pm$ 1.016	46-54	6.212 $\pm$ 1.237
46-48	2.079 $\pm$ .558	46-50	3.906 $\pm$ .822		
48-50	2.436 $\pm$ .707	50-54	5.162 $\pm$ .856		
Means	2.490 .610	3.865 .909		5.146 1.307	

Table 5-6. Partial regression coefficients of egg mass (EM) on metabolizable energy intake (ME) using 2-week, 4-week, and 8-week periods.

2-Week		4-Week		8-Week	
Age	EM	Age	EM	Age	EM
26-28	2.170 $\pm$ .245	26-30	2.125 $\pm$ .227	26-34	2.161 $\pm$ .231
28-30	1.649 $\pm$ .214	28-32	2.012 $\pm$ .221	28-36	2.294 $\pm$ .213
30-32	1.966 $\pm$ .236	30-34	2.233 $\pm$ .217	30-38	2.516 $\pm$ .199
32-34	2.027 $\pm$ .202	32-36	2.202 $\pm$ .209	32-40	2.427 $\pm$ .185
34-36	2.128 $\pm$ .228	34-38	2.410 $\pm$ .201	34-42	2.528 $\pm$ .186
36-38	2.239 $\pm$ .209	36-40	2.552 $\pm$ .192	36-44	2.637 $\pm$ .170
38-40	2.360 $\pm$ .224	38-42	2.453 $\pm$ .191	38-46	2.530 $\pm$ .190
40-42	2.136 $\pm$ .185	40-44	2.260 $\pm$ .184	40-48	2.460 $\pm$ .202
42-44	2.118 $\pm$ .212	42-46	2.314 $\pm$ .223	42-50	2.640 $\pm$ .213
44-46	2.006 $\pm$ .228	44-48	2.526 $\pm$ .220	46-54	2.714 $\pm$ .223
46-48	2.378 $\pm$ .231	46-50	2.671 $\pm$ .233		
48-50	2.242 $\pm$ .289	50-54	2.733 $\pm$ .220		
Means	2.118 .225	2.374 .212		2.491 .201	

Heritability estimates of metabolizable energy intake adjusted for metabolic body weight, body weight change, and egg mass output calculated from sire plus dam components of variance on the average were highest for the 8-week periods and lowest for the 2-week periods (Table 5-7). This was expected since 8-week periods showed the highest  $R^2$  and 2-week periods showed the lowest  $R^2$  for the reduced model (Table 5-3). Heritability of the residual is the percentage of the additive genetic variance to the total variance unexplained by the reduced model. The higher the  $R^2$  of the reduced model the higher the heritability estimate. Arboleda et al. (1976), who found a low heritability of 0.15 from the sire plus dam component of variance, reported a coefficient of determination for the reduced model to be between 0.40 and 0.51. The fact that they did not include the change in body weight in their reduced model may partially explain the lower  $R^2$ . Hagger and Abplanalp (1978) found  $R^2$  to be between 0.50 and 0.72 and the heritability estimates to be between 0.22 and 0.64.

The width of the range of the 4-week heritability estimates, which is the difference between the highest and the lowest estimate, was the lowest (.807-.160=.647), whereas 2-week and 8-week were .748 and .718, respectively. Only 4-week heritability estimates will be discussed.

Heritability estimates of residual component of energy intake calculated from sire plus dam components of variance ranged from .160 to .807 with a tendency for higher estimates from periods immediately following peak output of egg mass. Bentsen (1982) reported higher heritability estimates for the residual component of feed consumption during the peak of laying period in White Leghorn layers. Wing and

Table 5-7. Estimates of heritability and standard errors from sire plus dam components of variance for the residual components of energy intake.

2-Week			4-Week			8-Week		
Age	#	S+D	Age	#	S+D	Age	#	S+D
26-28	335	.237 $\pm$ .169	26-30	331	.292 $\pm$ .173	26-34	319	.251 $\pm$ .177
28-30	331	.339 $\pm$ .173	28-32	321	.242 $\pm$ .175	28-36	313	.271 $\pm$ .183
30-32	321	.159 $\pm$ .173	30-34	319	.230 $\pm$ .177	30-38	297	.566 $\pm$ .191
32-34	320	.451 $\pm$ .177	32-36	314	.391 $\pm$ .182	32-40	284	.792 $\pm$ .185
34-36	316	.336 $\pm$ .180	34-38	299	.639 $\pm$ .186	34-42	285	.827 $\pm$ .182
36-38	305	.523 $\pm$ .188	36-40	292	.807 $\pm$ .180	36-44	288	.889 $\pm$ .177
38-40	301	.616 $\pm$ .184	38-42	300	.775 $\pm$ .178	38-46	293	.829 $\pm$ .180
40-42	304	.766 $\pm$ .176	40-44	301	.650 $\pm$ .185	40-48	289	.551 $\pm$ .197
42-44	308	.394 $\pm$ .190	42-46	304	.561 $\pm$ .190	42-50	291	.519 $\pm$ .200
44-46	318	.359 $\pm$ .185	44-48	310	.305 $\pm$ .191	46-54	304	.171 $\pm$ .192
46-48	315	.253 $\pm$ .186	46-50	310	.215 $\pm$ .188			
48-50	313	.018 $\pm$ .180	50-54	319	.160 $\pm$ .180			
Means		.371 .180			.439 .182			.567 .186

Nordskog (1982a) reported heritabilities of .25 and .30 calculated from the sire plus dam components of variance of two White Leghorn Layer flocks. Bentsen (1982) estimated heritabilities from the sire plus dam components of variance to be between .12 to .56 for White Leghorn and between .00 to .51 for Rhode Island Red.

Both Hagger and Abplanalp (1978) and Bentsen (1982) observed a tendency for lower estimates of heritability of the residual from older birds. The last two periods (Table 5-7) showed lower estimates. However, our study ended at 54 weeks of age, which is earlier than the 60 and 66 weeks of age considered in the other two studies, respectively.

Heritability estimates of the partial regression coefficients of MEI on BW and EM were .705 ( $\pm$  .441) and .604 ( $\pm$  .636), respectively. Large standard errors could be due partially to limited amount of data.

High heritability estimates for the residual component of metabolizable energy intake suggest that selection for this trait could improve efficiency of egg production, and that high heritability estimates can be obtained using a short test period by measuring the residual during the few weeks immediately following peak output of egg mass. A possibility of using regression coefficients of metabolizable energy intake on body weight and egg mass as selection criteria for separately improving maintenance efficiency and egg production efficiency also is indicated.



## CHAPTER 6

### SUMMARY AND CONCLUSIONS

Feed efficiency is a major concern for egg production industry; however, the most common source of gain in feed efficiency has been increased egg production. Reducing layer body size also has contributed to feed efficiency improvement. Improving efficiency as a correlated response, however, has limits since gains in egg production tend to a plateau and small-bodied birds tend to lay smaller eggs. Thus it is of interest to consider that part of variability in feed intake which is independent of egg production and body size, or the residual.

The residual component of metabolizable energy intake is measured as the deviation between observed and expected metabolizable energy. The expected metabolizable energy can be estimated from a multiple regression equation with metabolizable energy intake as the dependent variable and metabolic weight, weight gain, and egg mass output as independent variables.

The objectives of this study were 1) to examine the residual component of metabolizable energy intake in comparison with other methods of measuring feed efficiency within a group of hens; 2) to compare energy utilization for maintenance and egg production by comparing the partial regression coefficients for maintenance and egg production among six different genetic lines; and 3) to study the effect

of several environmental factors on the residual and its heritability estimates. This study included three phases.

In the first phase 104 hens were used to study the relationship among different measurements of feed efficiency. Feed conversion, the ratio of feed consumption to egg mass output, was 2.06. Gross efficiency, percentage of total energy consumed converted to eggs was 23.71%. Correlation of  $-.93$  was found between feed conversion and gross efficiency. The correlations between the residual and feed conversion and gross efficiency were  $.41$  and  $-.55$ , respectively. Variation in metabolizable energy intake among individual hens, which could not be explained by the differences in body weights, changes in body weights, and egg mass output was observed.

In the second phase 180 hens from six different White Leghorn lines (30 birds/line) were used. The lines differed significantly ( $p < .05$ ) in their metabolizable energy intake, body weight, and egg mass output. Significant differences among the lines in efficiency were detected using feed conversion. A multiple regression equation was derived for each line. Significant differences were observed in the partial regression coefficients for maintenance.

In the last phase 335 pedigreed White Leghorn type hens, 26 weeks of age were used. During the 28-week experimental period the hens gained about 100 g. Egg mass output peaked at 36 weeks of age. Metabolic body weights, body weight changes, and egg masses produced accounted for 62.9%, 69.1%, and 72.1% of the total variation in metabolizable energy intake when 2-week, 4-week, and 8-week periods were used, respectively. Heritability estimates of the residual calculated

from the sire plus dam components of variance on the average were .37, .44, and .57 for the 2-week, 4-week, and 8-week periods, respectively. Higher heritabilities were obtained during the higher egg masses output periods and lower heritabilities at the older age, regardless of test period length used.

Variation in metabolizable energy intake among individual hens, which could not be explained by the differences in body weights, changes in body weights, and egg masses output was observed. The variation in the residuals might be due partially to variation in physiological factors such as basal metabolic rate and regulation of appetite. The significant differences in the partial regression coefficients for maintenance among the different genetic lines demonstrated the genetic differences in feed utilization for maintenance among the lines.

High heritability estimates for the residual component of metabolizable energy intake suggest that selection for this trait could improve the efficiency of egg production, and that high heritability estimates can be obtain using a short test period by measuring the residual during the few weeks immediately following peak output of egg mass. A possibility of using the regression coefficients of metabolizable energy intake on body weight and egg mass as selection criteria for separately improving maintenance efficiency and egg production efficiency also is indicated.

## APPENDIX

Table A-1. Estimates of heritability and standard errors from sire plus dam components of variance for metabolizable energy intake (Experiment 3, Chapter 5).

2-Week			4-Week			8-Week		
Age	#	S+D	Age	#	S+D	Age	#	S+D
26-28	335	.517 $\pm$ .168	26-30	331	.801 $\pm$ .161	26-34	319	.844 $\pm$ .162
28-30	331	.882 $\pm$ .156	28-32	321	.833 $\pm$ .162	28-36	313	.814 $\pm$ .167
30-32	321	.609 $\pm$ .171	30-34	319	.699 $\pm$ .170	30-38	297	.783 $\pm$ .178
32-34	320	.646 $\pm$ .171	32-36	314	.724 $\pm$ .172	32-40	284	.782 $\pm$ .183
34-36	316	.723 $\pm$ .170	34-38	299	.756 $\pm$ .178	34-42	285	.769 $\pm$ .183
36-38	305	.628 $\pm$ .182	36-40	292	.713 $\pm$ .183	36-44	288	.772 $\pm$ .182
38-40	301	.744 $\pm$ .176	38-42	300	.746 $\pm$ .177	38-46	293	.848 $\pm$ .176
40-42	304	.758 $\pm$ .175	40-44	301	.831 $\pm$ .173	40-48	289	.814 $\pm$ .181
42-44	308	.730 $\pm$ .178	42-46	304	.873 $\pm$ .171	42-50	291	.877 $\pm$ .178
44-46	318	.843 $\pm$ .167	44-48	310	.748 $\pm$ .177	46-54	304	.730 $\pm$ .180
46-48	315	.682 $\pm$ .176	46-50	310	.781 $\pm$ .174			
48-50	313	.744 $\pm$ .174	50-54	319	.633 $\pm$ .175			
Means		.709 .172			.762 .173			.803 .177

Table A-2. Estimates of heritability and standard errors from sire plus dam components of variance for body weight (Experiment 3, Chapter 5).

2-Week			4-Week			8-Week		
Age	#	S+D	Age	#	S+D	Age	#	S+D
26-28	335	.988 $\pm$ .146	26-30	331	1.025 $\pm$ .145	26-34	319	1.020 $\pm$ .149
28-30	331	1.035 $\pm$ .145	28-32	321	1.004 $\pm$ .150	28-36	313	1.020 $\pm$ .152
30-32	321	1.050 $\pm$ .146	30-34	319	1.021 $\pm$ .149	30-38	297	.971 $\pm$ .164
32-34	320	.948 $\pm$ .155	32-36	314	.946 $\pm$ .158	32-40	284	.807 $\pm$ .181
34-36	316	.934 $\pm$ .157	34-38	299	.863 $\pm$ .171	34-42	285	.831 $\pm$ .179
36-38	305	.911 $\pm$ .166	36-40	292	.870 $\pm$ .173	36-44	288	.857 $\pm$ .177
38-40	301	.737 $\pm$ .177	38-42	300	.797 $\pm$ .174	38-46	293	.653 $\pm$ .187
40-42	304	.727 $\pm$ .176	40-44	301	.660 $\pm$ .182	40-48	289	.739 $\pm$ .185
42-44	308	.720 $\pm$ .178	42-46	304	.670 $\pm$ .183	42-50	291	.820 $\pm$ .182
44-46	318	.716 $\pm$ .174	44-48	310	.813 $\pm$ .173	46-54	304	.815 $\pm$ .175
46-48	315	.834 $\pm$ .168	46-50	310	.869 $\pm$ .168			
48-50	313	.907 $\pm$ .164	50-54	319	.865 $\pm$ .163			
Means		.876 .163			.867 .166			.853 .173

Table A-3. Estimates of heritability and standard errors from sire plus dam components of variance for body weight change (Experiment 3, Chapter 5).

2-Week			4-Week			8-Week		
Age	#	S+D	Age	#	S+D	Age	#	S+D
26-28	335	.000 $\pm$ .000	26-30	331	.265 $\pm$ .170	26-34	319	.000 $\pm$ .000
28-30	331	.028 $\pm$ .161	28-32	321	.391 $\pm$ .174	28-36	313	.177 $\pm$ .176
30-32	321	.000 $\pm$ .000	30-34	319	.000 $\pm$ .000	30-38	297	.000 $\pm$ .000
32-34	320	.000 $\pm$ .000	32-36	314	.241 $\pm$ .178	32-40	284	.048 $\pm$ .191
34-36	316	.177 $\pm$ .175	34-38	299	.017 $\pm$ .181	34-42	285	.263 $\pm$ .195
36-38	305	.000 $\pm$ .000	36-40	292	.000 $\pm$ .000	36-44	288	.017 $\pm$ .188
38-40	301	.000 $\pm$ .000	38-42	300	.093 $\pm$ .182	38-46	293	.081 $\pm$ .189
40-42	304	.000 $\pm$ .000	40-44	301	.011 $\pm$ .180	40-48	289	.499 $\pm$ .195
42-44	308	.332 $\pm$ .187	42-46	304	.205 $\pm$ .189	42-50	291	.507 $\pm$ .197
44-46	318	.000 $\pm$ .000	44-48	310	.500 $\pm$ .186	46-54	304	.374 $\pm$ .190
46-48	315	.034 $\pm$ .176	46-50	310	.197 $\pm$ .184			
48-50	313	.262 $\pm$ .184	50-54	319	.355 $\pm$ .180			
Means		.069 .074			.190 .150			.197 .152

Table A-4. Estimates of heritability and standard errors from sire plus dam components of variance for egg mass output (Experiment 3, Chapter 5).

2-Week			4-Week			8-Week		
Age	#	S+D	Age	#	S+D	Age	#	S+D
26-28	335	.584 $\pm$ .167	26-30	331	.693 $\pm$ .166	26-34	319	.503 $\pm$ .175
28-30	331	.646 $\pm$ .167	28-32	321	.552 $\pm$ .173	28-36	313	.263 $\pm$ .179
30-32	321	.357 $\pm$ .174	30-34	319	.192 $\pm$ .173	30-38	297	.058 $\pm$ .185
32-34	320	.000 $\pm$ .000	32-36	314	.040 $\pm$ .171	32-40	284	.030 $\pm$ .190
34-36	316	.180 $\pm$ .175	34-38	299	.056 $\pm$ .183	34-42	285	.056 $\pm$ .190
36-38	305	.017 $\pm$ .179	36-40	292	.030 $\pm$ .185	36-44	288	.104 $\pm$ .192
38-40	301	.144 $\pm$ .184	38-42	300	.126 $\pm$ .183	38-46	293	.109 $\pm$ .190
40-42	304	.104 $\pm$ .180	40-44	301	.165 $\pm$ .185	40-48	289	.184 $\pm$ .195
42-44	308	.148 $\pm$ .184	42-46	304	.164 $\pm$ .188	42-50	291	.196 $\pm$ .198
44-46	318	.130 $\pm$ .179	44-48	310	.264 $\pm$ .187	46-54	304	.327 $\pm$ .190
46-48	315	.445 $\pm$ .183	46-50	310	.523 $\pm$ .184			
48-50	313	.478 $\pm$ .183	50-54	319	.179 $\pm$ .179			
Means		.269 .163			.249 .180			.183 .188



Table A-5. Estimates of heritability and standard errors from sire components of variance for metabolizable energy intake (Experiment 3, Chapter 5).

2-Week			4-Week			8-Week		
Age	#	S+D	Age	#	S+D	Age	#	S+D
26-28	335	.344 $\pm$ .177	26-30	331	.443 $\pm$ .190	26-34	319	.472 $\pm$ .198
28-30	331	.432 $\pm$ .189	28-32	321	.451 $\pm$ .195	28-36	313	.462 $\pm$ .199
30-32	321	.356 $\pm$ .184	30-34	319	.427 $\pm$ .193	30-38	297	.526 $\pm$ .213
32-34	320	.376 $\pm$ .187	32-36	314	.419 $\pm$ .194	32-40	284	.644 $\pm$ .230
34-36	316	.456 $\pm$ .198	34-38	299	.515 $\pm$ .211	34-42	285	.648 $\pm$ .229
36-38	305	.457 $\pm$ .202	36-40	292	.633 $\pm$ .225	36-44	288	.649 $\pm$ .228
38-40	301	.640 $\pm$ .222	38-42	300	.586 $\pm$ .217	38-46	293	.669 $\pm$ .228
40-42	304	.355 $\pm$ .190	40-44	301	.552 $\pm$ .213	40-48	289	.654 $\pm$ .228
42-44	308	.619 $\pm$ .217	42-46	304	.681 $\pm$ .224	42-50	291	.774 $\pm$ .237
44-46	318	.544 $\pm$ .206	44-48	310	.647 $\pm$ .219	46-54	304	.547 $\pm$ .212
46-48	315	.719 $\pm$ .224	46-50	310	.715 $\pm$ .225			
48-50	313	.608 $\pm$ .214	50-54	319	.373 $\pm$ .187			
Means		.492 .201			.537 .208			.605 .220

Table A-6. Estimates of heritability and standard errors from sire components of variance for body weight (Experiment 3, Chapter 5).

2-Week			4-Week			8-Week		
Age	#	S+D	Age	#	S+D	Age	#	S+D
26-28	335	.551 $\pm$ .201	26-30	331	.561 $\pm$ .203	26-34	319	.546 $\pm$ .206
28-30	331	.645 $\pm$ .211	28-32	321	.617 $\pm$ .212	28-36	313	.755 $\pm$ .227
30-32	321	.610 $\pm$ .212	30-34	319	.620 $\pm$ .213	30-38	297	.712 $\pm$ .230
32-34	320	.571 $\pm$ .208	32-36	314	.669 $\pm$ .220	32-40	284	.643 $\pm$ .229
34-36	316	.641 $\pm$ .216	34-38	299	.630 $\pm$ .222	34-42	285	.655 $\pm$ .230
36-38	305	.725 $\pm$ .228	36-40	292	.722 $\pm$ .233	36-44	288	.774 $\pm$ .239
38-40	301	.572 $\pm$ .215	38-42	300	.591 $\pm$ .218	38-46	293	.715 $\pm$ .232
40-42	304	.577 $\pm$ .215	40-44	301	.610 $\pm$ .219	40-48	289	.756 $\pm$ .237
42-44	308	.602 $\pm$ .215	42-46	304	.695 $\pm$ .226	42-50	291	.794 $\pm$ .239
44-46	318	.738 $\pm$ .224	44-48	310	.745 $\pm$ .228	46-54	304	.884 $\pm$ .240
46-48	315	.725 $\pm$ .224	46-50	310	.809 $\pm$ .233			
48-50	313	.858 $\pm$ .235	50-54	319	.904 $\pm$ .236			
Means		.651 .217			.681 .222			.723 .231

Table A-7. Estimates of heritability and standard errors from sire components of variance for body weight change (Experiment 3, Chapter 5).

2-Week			4-Week			8-Week		
Age	#	S+D	Age	#	S+D	Age	#	S+D
26-28	335	.054 $\pm$ .137	26-30	331	.000 $\pm$ .000	26-34	319	.000 $\pm$ .000
28-30	331	.000 $\pm$ .000	28-32	321	.000 $\pm$ .000	28-36	313	.092 $\pm$ .153
30-32	321	.000 $\pm$ .000	30-34	319	.000 $\pm$ .000	30-38	297	.000 $\pm$ .000
32-34	320	.000 $\pm$ .000	32-36	314	.291 $\pm$ .179	32-40	284	.209 $\pm$ .182
34-36	316	.380 $\pm$ .189	34-38	299	.128 $\pm$ .165	34-42	285	.340 $\pm$ .198
36-38	305	.003 $\pm$ .143	36-40	292	.000 $\pm$ .000	36-44	288	.203 $\pm$ .179
38-40	301	.152 $\pm$ .166	38-42	300	.153 $\pm$ .166	38-46	293	.216 $\pm$ .178
40-42	304	.004 $\pm$ .142	40-44	301	.037 $\pm$ .149	40-48	289	.536 $\pm$ .217
42-44	308	.110 $\pm$ .156	42-46	304	.192 $\pm$ .170	42-50	291	.802 $\pm$ .239
44-46	318	.000 $\pm$ .000	44-48	310	.385 $\pm$ .192	46-54	304	.439 $\pm$ .201
46-48	315	.085 $\pm$ .151	46-50	310	.362 $\pm$ .189			
48-50	313	.123 $\pm$ .157	50-54	319	.206 $\pm$ .166			
Means		.076 .103			.146 .115			.284 .155

Table A-8. Estimates of heritability and standard errors from sire components of variance for egg mass output (Experiment 3, Chapter 5).

2-Week			4-Week			8-Week		
Age	#	S+D	Age	#	S+D	Age	#	S+D
26-28	335	.234 $\pm$ .163	26-30	331	.192 $\pm$ .159	26-34	319	.128 $\pm$ .155
28-30	331	.051 $\pm$ .139	28-32	321	.093 $\pm$ .149	28-36	313	.085 $\pm$ .152
30-32	321	.147 $\pm$ .157	30-34	319	.078 $\pm$ .148	30-38	297	.119 $\pm$ .164
32-34	320	.015 $\pm$ .138	32-36	314	.086 $\pm$ .151	32-40	284	.090 $\pm$ .166
34-36	316	.171 $\pm$ .162	34-38	299	.127 $\pm$ .164	34-42	285	.068 $\pm$ .162
36-38	305	.072 $\pm$ .154	36-40	292	.060 $\pm$ .157	36-44	288	.000 $\pm$ .000
38-40	301	.050 $\pm$ .151	38-42	300	.035 $\pm$ .149	38-46	293	.000 $\pm$ .000
40-42	304	.000 $\pm$ .000	40-44	301	.000 $\pm$ .000	40-48	289	.000 $\pm$ .000
42-44	308	.000 $\pm$ .000	42-46	304	.000 $\pm$ .000	42-50	291	.030 $\pm$ .153
44-46	318	.000 $\pm$ .000	44-48	310	.000 $\pm$ .000	46-54	304	.065 $\pm$ .153
46-48	315	.000 $\pm$ .000	46-50	310	.000 $\pm$ .000			
48-50	313	.000 $\pm$ .000	50-54	319	.321 $\pm$ .181			
Means		.062 .089			.083 .105			.059 .111

Table A-9. Estimates of heritability and standard errors from sire components of variance for the residual of metabolizable energy intake (Experiment 3, Chapter 5).

2-Week			4-Week			8-Week		
Age	#	S+D	Age	#	S+D	Age	#	S+D
26-28	335	.482 $\pm$ .193	26-30	331	.589 $\pm$ .206	26-34	319	.530 $\pm$ .204
28-30	331	.622 $\pm$ .209	28-32	321	.555 $\pm$ .206	28-36	313	.403 $\pm$ .193
30-32	321	.411 $\pm$ .190	30-34	319	.477 $\pm$ .199	30-38	297	.568 $\pm$ .217
32-34	320	.425 $\pm$ .193	32-36	314	.229 $\pm$ .171	32-40	284	.654 $\pm$ .230
34-36	316	.066 $\pm$ .147	34-38	299	.434 $\pm$ .202	34-42	285	.698 $\pm$ .234
36-38	305	.585 $\pm$ .215	36-40	292	.629 $\pm$ .225	36-44	288	.708 $\pm$ .233
38-40	301	.405 $\pm$ .198	38-42	300	.643 $\pm$ .223	38-46	293	.609 $\pm$ .222
40-42	304	.533 $\pm$ .210	40-44	301	.619 $\pm$ .220	40-48	289	.453 $\pm$ .208
42-44	308	.469 $\pm$ .202	42-46	304	.457 $\pm$ .202	42-50	291	.268 $\pm$ .186
44-46	318	.266 $\pm$ .176	44-48	310	.307 $\pm$ .183	46-54	304	.391 $\pm$ .195
46-48	315	.392 $\pm$ .191	46-50	310	.206 $\pm$ .170			
48-50	313	.102 $\pm$ .154	50-54	319	.355 $\pm$ .185			
Means		.397 .190			.458 .199			.528 .212

Table A-10. Means and standard errors for age and body weight at sexual maturity (Experiment 3, Chapter 5).

#	Age at sexual maturity	Body weight at sexual maturity
335	173.9 $\pm$ .6	1352.5 $\pm$ 4.6

Table A-11. Estimates of heritability and standard errors for age and body weight at sexual maturity (Experiment 3, Chapter 5).

#	Age at sexual maturity	Body weight at sexual maturity
From sire plus dam components of variance:		
335	.387 $\pm$ .169	.623 $\pm$ .166
From sire components of variance:		
335	.345 $\pm$ .177	.438 $\pm$ .188

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